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GEOGRAPHIC VARIATION IN BIRDS WITH ESPECIAL REFERENCE TO THE EFFECTS OF HUMIDITY

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GEOGRAPHIC VARIATION IN BIRDS.

WITH ESPECIAL REFERENCE TO THE EFFECTS OF HUMIDITY.

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PART I.—HISTORICAL.

It has long been known that many mammals, birds and reptiles inhabiting a moist, humid region show a much darker or increased pigmentation of the hair, feathers or scales than individuals from dryer localities. In cases where there are barriers isolating the humid forms, they are recognized as of specific or of subspecific value. Even where perfectly continuous intergradations are found, reflecting the gradual transition from lesser to greater humidity, each extreme type of the series, and occasionally several central forms, are differentiated by the systematist.

Correlated with this darkening of the epidermal structures, is frequently a distinction in point of size, either of the body and skeleton as a whole, or superficially, as of longer or shorter feathers of the wings and tail. The two best known and most often quoted examples among birds in our own country are *Colinus* and *Melospiza*—the bob-whites and song sparrows. Certain species of the mammalian genera *Canis* and *Sciurus*—wolves and squirrels, show this regional or climatal variation well, and among the reptilia, *Eutaenia* and *Crotalus*—the garter and rattle snakes—are especially susceptible to climatic influences.

These facts of distributional variation were enunciated anew in a recent interesting discussion in *Science*, from which I shall quote a few significant paragraphs.

Speaking of the climatic or geographic variation mentioned above, Dr. J. A. Allen says:—"Secondly, and coincidently with the decrease in size southward, is a change in coloration, which may be described in general terms as a restriction in area of all white markings and a corresponding increase in the area of the dark markings, together with, generally speaking, an increase in the intensity of color in markings or areas of other tints than black or white, as yellows, greens, browns, etc., and also in iridescence, in birds of metallic tints. * * *

"It is equally well known that in continently dispersed groups, pallid tints accompany desert areas and arid conditions of climate, and that increase in depth of color, particularly in gray, brown and olive tints, is an inseparable accompaniment of regions of heavy rainfall and a moist climate, so familiarly illustrated in the northwest coast region of North America. * * * In other words, regional areas of peculiar climatic conditions impress upon their animal inhabitants a certain distinctive phase of coloration, developing in some instances wholly new specific types, in others merely forms that intergrade with others of the immediately adjoining districts."

Near the end of the same article we read that Dr. Allen believes that the evolution of species and races has been brought about chiefly by environment, as opposed to natural selection—used in the original restricted sense—and that the main factor in this evolution is climate.

Two months later in a second article Dr. Allen thus argues for the inheritance of local differences in color of subspecific value:

"Young mammals in the nursling stage have a pelage different in color and texture from that later acquired; young birds have a characteristic nestling plumage different in color and texture from that of the adults, or from that acquired with the first moult. Every experienced mammalogist and ornithologist knows that the local differentiation in color between the subspecific forms of a group is often—but not always—much more strongly expressed in the first pelage or plumage of the young than in the adults of the same forms. In view of such facts it seemingly goes without saying that local differentiations are transmitted from parent to young, and are hereditary in the usual sense of that term; doubtless no one questions their continued transmission from generation to generation so long as the environment remains stable. Probably also few would question that were representatives of a strongly marked local form—in the case of birds, either as eggs or mature birds—to be trans-

planted to a region markedly different climatically from their natural home, they would gradually lose their original characteristics, and become, after a number of generations, more or less modified, in better agreement with the new conditions of life. But it would be apparently rash to expect a very material change in a single generation. There is apparently not the least probability that an egg of a large dusky Vancouver woodpecker taken to Arizona would hatch into a smaller pale form like the race native to Arizona."

Dr. Allen then goes on to tell of the stocking of northern preserves with the smaller, darker bob-whites from localities farther south, and states that no change in size or color has been observed. The same is said to be true of the bob-whites—supposedly Floridian—which, one hundred years ago, were introduced into Cuba, although there are now found in Cuba "quail that are intermediate in characters between the true Cuban form and the Florida form, due possibly to interbreeding but also possibly to the action of environment upon the introduced Florida stock."

In a continuation of this discussion in a later number of *Science*, Prof. T. D. A. Cockerell writes in the concluding paragraph of his article, "Finally, it is by no means to be assumed that the 'effects' of climate are necessarily direct, and not brought about through the agency of natural selection."

In a note at the conclusion of a paper on "The Variation of *Eutaenia* in the Pacific Subregion" Mr. A. E. Brown says, "That humidity in some way influences the metabolic processes which lead to pigmentation can hardly be doubted. Temperature need scarcely be considered in the present case, for the dry region, extending from Arizona to northern Montana, and to considerable elevations, has a very great thermal range, while the wet region is relatively equable. There is a suggested connection between the large amount of uric acid produced by reptiles and the fact that the yellow and orange coloring matter from the wings of certain butterflies has yielded a substance closely related to uric acid, but physiological chemistry is not yet competent to explain how these waste products are converted into pigments."

Folsom contends in the case of insects that the "effects of climatal influences and of nutrition are frequently adaptive and often transmissible, as experiments have proved. There is, however, much difference of opinion as to the precise way in which these effects are transmitted."

"Upon members of the Animal Kingdom," writes Dr. H.

M. Vernon, "observations as to the effect of moisture are exceedingly meagre. This is probably attributable to the fact that in most cases a direct effect is either slight or wanting. * * * In any case, the effect is probably an indirect one, acting through the vegetation."

In the summary of a series of thorough and very significant experiments relating to the effects of temperature and moisture on various species of the Coleopteran genus *Leptinotarsa*, Prof. W. L. Tower draws the following conclusions which he believes hold good for all insects.

1—The different factors of the environmental complex do not have any specific influence upon coloration, but all act alike as stimuli, either alone or in combinations, to accelerate or retard color development, and thus to modify coloration in the following ways:

a—Toward melanic or albinic conditions, which are the most general and important in coloration.

b—Toward suppression or accentuation of particular color areas or groups thereof.

c—Toward changes in the colors themselves.

2—The factors most potent in the modification of coloration are temperature and moisture; soil and altitude act indirectly through moisture and temperature, while the influence of food, light, and other factors is very slight.

3—Any factor acting as a stimulus produces at once the maximum response which the deviation in the factor is capable of producing, and this maximum response remains constant as long as the stimulus is in force, but varies as the stimulus varies, and is lost when the stimulus is removed.

4—Any factor which deviates either above or below the normal has the effect up to a certain point of producing increased pigmentation, and beyond that point of retarding it.

5—Variations produced by the action of environmental factors during ontogeny always follow the laws of fluctuating variations. New combinations of color characters never appear as the result of stimuli applied during ontogeny, and the modifications found are all in the line of accentuation or reduction of the color characters natural to the species.

6—The variations produced in experiment resemble in their polygons of distribution and in their modal classes conditions found in nature in places or in seasons in which the conditions of existence are similar to those of the experiment; and a variation found in nature is to be interpreted as the result of a devi-

ation of some factor of the environment acting as a stimulus to produce a modification of coloration.

7—The variations produced by somatic stimuli are never inherited, no matter how long the stimuli be applied. They are therefore of no importance in evolution. They are of importance, however, in a consideration of the phenomena of place and geographical variation.

8—Species of high variability in nature are also highly variable in experiment, and conversely, those which are constant in nature are the same in experiment; hence the observed variability of a species is a good index of the presence or absence of somatic plasticity but is not necessarily an indication of its ability to produce germinal variations and become a factor in evolution.

“Permanent, heritable color modifications of *Leptinotarsa* have been found in nature, and are indistinguishable from somatic variations excepting in their capacity for being transmitted to subsequent generations. They, however, have no relation to the variations experimentally induced herein described.”

Writing of the mutation theory in animal evolution, Prof. Davenport mentions black plumage and color of iris among other “discontinuous characteristics,” and goes on to say, “One who sees the striking failure of these characteristics and many others to be modified in any important way will feel convinced that they are not capable of forming intergrades, and hence could not have arisen gradually.”

I have quoted from these various authorities in full to show what diverse views on the subject are at present rife among biologists, and how little we actually know not only of the direct action of the various climatic factors of the environment, such as temperature, humidity and light, upon terrestrial vertebrates, but of the relative importance of these factors both in the ontogenetic and phylogenetic history of the various organisms. The most important phase of the subject and the one about which, if possible, we know least, is the difference of inception and assimilation of the various externally exerted stimuli, bringing about non-inheritable somatic variations on the one hand, and on the other, the heritable variations of the germ plasm; both, in many cases, superficially so similar, and yet in their cumulative influence so radically unlike in relative importance.

Concerning the radical effects of a new environment acting within historical times, Darwin relates of the Porto Santo rabbits, that in less than 440 years they had “decreased nearly three inches in length and almost half in weight of body,” besides

changing considerably in color, especially in the ears and tail; these being reddish-brown instead of blackish. But when one of these feral rabbits, which had been confined for some time in the London Zoo, died and was examined, it was found that "under the English climate this individual rabbit had recovered the proper color of its fur in rather less than four years!"

In this instance, although the details are meagre enough, we have conclusive evidence of a radical—and to all intents, specific—change of color in the life-time of one individual, and a most surprising change in size and weight of the entire organism during a period of about 400 years.

In regard to the effect of humidity on insects, Marshall and Poulton, writing of the dimorphic seasonal forms of certain butterflies in South Africa, regard this as due to the alternation of dry and rainy seasons which there take the place of summer and winter.

Changes in the imago of moths and butterflies have been experimentally induced by subjecting both caterpillars and chrysalides to intense humidity. The artificial melanism induced in beetles of the genus *Leptinotarsa* by Tower has already been mentioned.

Dr. Allen in his article on Heredity and Subspecies, from which I have quoted, does not mention the instance of the bob-white in Jamaica. This bird, according to Gosse, was introduced upon the island from North America about 1747. As a whole, the race has been almost exterminated by the naturalized mongoose. I have recently received an interesting living specimen of the bob-white from this island, thus representative of an isolated island colony established 160 years ago. Difficult as comparisons are when the subject is alive and energetic, and when its rarity renders even a cursory handling very dangerous, I have made as careful an examination as possible, and compared it as regards color and measurements with typical specimens from the north and from Florida.

In the Jamaica bob-white, a male bird, the white forehead and superciliary stripe are variegated with black, and the red on the head, while very intense, is confined to the extreme tips of the feathers. In a typical northern bird in unworn plumage the red on these crown feathers comprises some 5 mm. of the distal portion, while in the Jamaica bird this color is reduced to 2 mm.

The ear-coverts and sides of the head are almost uniformly black, while the throat is variegated, being about half white and half black. No intermediate grays are present here, the two ex-

tremes of color being in sharp contrast to each other. The black cervical band is very wide. The greater wing coverts, instead of showing vague slate-colored markings, are crossed by clear-cut transverse bars, while the doubly crescentic black bars on the feathers of the under parts are twice as broad in the Jamaica bird as in the typical northern bob-white.

Black predominates on the inner tertials and the buff edge-ings of these feathers are wide and very intense. The feathers of the back and tail coverts are dark, while the tail feathers themselves are almost black. Everywhere on the body and wings the red color, where not replaced with black, is deep and intense, a rich rufous much as in *Colinus cubanensis*. The wing of this bird measures 4.25 inches and the tail 2.25 inches, these measurements being considerably less than in birds from the north.

The quail flourished on the island until the mongoose was introduced, an animal which increased so rapidly as almost to exterminate the terrestrial mammal and bird fauna. The result of this is that to-day the quail are very rare, there being but two or three small covies scattered over two restricted districts. A recent observer estimates the total number of birds on the island at not over 70.

Although dark coloring in southern humid regions is often accompanied by a decrease in size, rarely by an increase, there is, as I think my experiments on *Scardafella* show, no necessary intimate correlation between the two phenomena. That of size may indicate, as Dr. Allen suggested thirty years ago, the course of adaptive radiation; the larger forms representing the hypothetical center of distribution. But size may or may not be significant of long existing conditions (cf. the Porto Santo rabbits, p. 7), while, as we shall see, geographical variations in color, even after long continued exposure of generations to an extreme of climate (*Scardafella inca*, in Mexico and Arizona) may prove to be of the most plastic and evanescent character.

PART II.—DICHROMATISM.

The more or less regular occurrence of black or dark-colored individuals among wild birds is known in many instances. From these I shall select a few of the more significant. The Old World snipe *Gallinago gallinago* ranges over Europe, Asia and North Africa. Fifty-five melanistic specimens are known in collections, so-called *G. sabinii*, of which thirty-one were taken in Ireland, twenty-two in England and one each in Scotland and on

the continent of Europe. Here we have an interesting case of the localization and the restriction to a humid region, of a melanistic form, race or variation, whatever we choose to call it in the present state of our knowledge. The rough-legged hawks and fulmar petrels, *Archibuteo* and *Fulmarus*, of America, and the parasitic jaeger, *Stercorarius parasiticus*, also exhibit a dark phase which is independent of age, sex or season.

A well known example of rather unique occurrence is found in *Pavo nigripennis*, the black-winged peacock, in which almost the entire wings and thighs are black. This form has never yet been observed in a wild state, but in flocks kept in semi-domestication, it occasionally crops out, and though weaker and less hardy than its parents, typical *Pavo cristatus*, yet it is said that if left to interbreed, this melanistic form will gradually become dominant and ultimately supplant all of the normally colored birds. Ogilvie-Grant says of this bird: "Although this variety closely resembles the male hybrids between *Pavo cristatus* and *P. muticus*, it has been clearly shown that it arises independently in flocks of common peafowl which have been pure bred for many years, and there can be no doubt that it is merely a sport of nature, possibly due to atavism or reversion to the ancestral type, from which both the common and the Burmese peafowl have sprung."

The black hawk, as the dark phase of the rough-legged hawk is called, *Archibuteo lagopus sancti-johannis*, while appearing during migration as isolated individuals all over the United States and southern Canada, seems to have a center of abundance in Ungava and Labrador. The Storers found the black hawk not uncommon on the cliffs of Labrador and their "observations of its habits, as contrasted with those of the still more common rough-legged hawk, left no doubt in their mind of their specific distinction. While the black hawk was observed to be a bold, vigorous and spirited bird, easy and swift in its motions, and preying upon other birds while on the wing, the rough-legged was comparatively sluggish, inoffensive and subsisted only upon rats, mice, moles, frogs and other small game. A nest containing young birds was found and one of the latter caught alive. Both old and young were in the same black plumage. The young hawk was fierce and intractable, and its whole air and manner were utterly unlike the conduct of the young of the other species." It is difficult to account for this reputed difference in mental character correlated with distinction in color phase, unless the observers were deceived by the marked individuality of a few birds.

Among many hundreds of rough-legged hawks sent to the Smithsonian Institution from the Arctic regions, not one was in the dark phase. But in the Ungava District, east of Hudson and James Bay, they are said to be common. Of one hundred birds killed within a short time at Toronto, five were black hawks. The extreme type of each phase has the young and adult plumage distinctly marked, but these are connected by individuals exhibiting every gradation of intermediate characters.

Although not dichromatic in the sense of the different color forms inhabiting the same regions, yet the common red-tailed hawk, *Buteo borealis*, should be mentioned here as a type of sub-specific geographic variation found in many groups of birds. In eastern North America this hawk is subject to comparatively little variation, but in the west and southward, through Mexico, it presents widely different phases. In the central United States a very light colored phase is known as the subspecies *krideri*, while a Pacific and Mexican melanistic and erythrystic phase has been named *calurus*. The young of all the forms appear to be indistinguishable and the adults differ from one another in neither size nor shape, but only in the pigmentation of the feathers.

As regards the group of jaegers or skuas, *Stercorarius*, dichromatism seems to exist in almost all. *S. pomarinus* has two very distinct color phases, one almost wholly sooty-brown, the other particolored, dark above and white on the breast. This condition is duplicated in *S. parasiticus* but in the closely related *S. longicaudus*, only one, the white phase, is commonly seen, although there is one record of a dark individual of this species.

In the two first mentioned species, a particolored bird may be frequently found mated with one wholly dark, in fact it is said that both partners are rarely alike in their phase of plumage. As in *Archibuteo*, the distinction depends neither upon age, sex nor season.

In the *Procellariiformes*, which include the albatrosses, fulmars and petrels, dichromatism is a common characteristic, as among *Ossifraga* and *Fulmarus*. In the latter birds an important fact is the tendency toward geographical isolation of the two phases, the dark phase, in both the Atlantic and Pacific birds, being predominant toward the west.

Uria troile, the common murre, has an interesting color phase which is said to occur in from one out of twenty to as high a ratio as one out of five individuals at the vast breeding rookeries of this species. These less numerous birds were formerly thought to be distinct and were named *ringvia* and *lacry-*

mans, but they are now recognized as only a color phase. In distinction to the others they have a white ring around the eye and a white stripe leading back from it. No intermediate types are known; the murre either possessing the circle and stripe fully developed or being wholly without it. On our coast the murre breeds along the sea-cliffs from Nova Scotia northward. It is said that in the Californian subspecies this white phase is never found, although it is present in birds of Europe and Asia.

The status of *Chen hyperboreus* and *C. caerulescens*, the snow and the blue goose, has long been a puzzle to systematists. *C. hyperboreus* is pure white in color with black tips to the primaries. The immature bird closely resembles *C. caerulescens*, having a light head and neck, but with all the upper body plumage dusky or bluish-gray. For many years the blue goose was thought to be merely the young of *C. hyperboreus*, but ultimately both were considered to be true species, and in the check-lists to-day are so listed. But word comes indirectly from Prof. F. E. Blaauw, of Holland, that he has obtained *C. caerulescens* from eggs laid by *C. hyperboreus*, and vice versa. This would indicate that, if indeed the two geese breed true and by themselves in the Arctic regions, one of the forms is of comparatively recent origin. We know nothing of the nest and eggs in nature of *C. caerulescens* except from the report of the Esquimo that its home is in the inaccessible *humid* bogs and swamps of the interior of Labrador. It is said that the blue goose "crosses James Bay, in the southern part of Hudson Bay, coming from the eastern coast, while the snow goose comes down from the north, seeming evidently to indicate that their breeding places are distinct."

If the various facts above related concerning these two forms of geese are correct, and if the intra-specific occurrence of such dichromatic phases as these, adumbrates new and permanent forms, we have an interesting and significant stage of species formation by geographical variation. The status of the forms of *Chen* may, from such a point of view, be considered as somewhat more advanced than the condition in *Gallinago*, *Archibuteo*, and, as we shall see later, in *Felis pardus*.

Although, and this is an important point, while in these latter forms the dark phase of distributional variation is subordinate to the normal type, and at the same time congenital and of recent evolution—perhaps an incipient species—in the case of *Chen* the fact that *hyperboreus* in its immature plumage closely resembles *caerulescens* would seem to indicate that the latter phase—or species—is the more primitive and ancient, and is per-

haps being supplanted by the white type.* In other words, if *Chen caerulescens* and the dark phase of *Gallinago gallinago* were bred in captivity from *C. hyperboreus* and from normally colored *Gallinago*, we should be inclined, in the present state of our knowledge, to consider the former an atavism, the latter a recent variation.

I have taken this theoretical point up in some detail to show the possibilities of species-formation from distributional variation—on the one hand (*Gallinago*) a humid phase evolving in a restricted locality from a widely spread typically colored species, and in the other case (*Chen*) a form, local at least in its present distribution, perhaps immediately ancestral to a lighter type of bird, which, in one or the other of its two intergrading subspecies (*C. hyperboreus* and *C. h. nivalis*), is circumpolar.

Examples which have apparently attained the final step in species demarcation, but which are separated specifically by only the single character of a difference in color, are the white and the scarlet ibises *Guara alba* and *G. rubra*, and the great white and the Ward heron *Ardea occidentalis* and *A. herodias wardi*. These are said to be specifically identical in all characters except the pigmentation of their feathers.

Ardea rufescens, the chestnut and bluish colored reddish egret and *Ardea pealei*, a pure white bird, were thought to be different species until the discovery of their interbreeding proved them to be only two phases of the same species. In this case, intermediate, particolored birds are not uncommon.

We shall pass over many other interesting cases of dichromatism in birds, and mention only *Falco sparverioides*, the Cuban sparrow hawk, which exhibits two very distinct color phases. I have had two living adult birds, one in the light and one in the dark phase, under observation for two years, having received them when they had not yet shed all their nestling down. With each succeeding moult there has been a more and more sharp demarcation between the coloration of the two types. The crown is the same color in both birds, but the pure cinnamon back of the light phase is so encroached upon by dark blue in the other bird, that the cinnamon is reduced to irregular and broken bars, present on only some of the feathers. In the dark bird the black area on all the wing feathers is increased and the parts of these feathers which are white in the light bird are

*The white color of the snow goose, homologous as it is with the same phenomenon in most other terrestrial Arctic birds and mammals, must not be confused with *albinism* to which it is in no way analogous. With this abnormal condition we have nothing to do in this paper.

wholly replaced with rufous in the other phase. In the dark bird, blue barring has appeared on the under primary coverts and subterminal spots on the feathers of the sides, while the entire under parts, from throat to tail coverts, is a deep cinnamon, very different from the white, slightly rusty-tinged, ventral feathering of the light bird.

Our knowledge of these two forms in the living wild state is very meagre. They have been known to breed together, and young birds of both colors have been found in the same nest, but Mr. Chapman records that of all the pairs he observed breeding in Cuba, in no case was a dark bird paired with a light one, or vice versa. The most interesting fact in regard to this dichromatic species is its extreme localization. Closely related forms of *Falco* are found throughout the other West India Islands and in most of North and South America, and yet outside of Cuba there is no tendency shown to develop distinct color phases.

To refer parenthetically to geographical melanism in the mammalia, we find a number of examples paralleling in many respects the avian case of *Gallinago*. Partial and wholly melanistic individuals of the jaguar, *Felis onca*, are not uncommon in northern South America, being most abundant, according to Humboldt, in the humid region of the Orinoco, while to the southward these animals become more yellowish or even whitish in color. It was formerly thought that this dark phase was a distinct species and the name *Felis nigra* was given to it by Erxleben. The best known case of melanism among mammals is the leopard, *Felis pardus*. Intermediate phases are rare, the melanism being usually so complete that the entire animal is uniformly black, the rosettes being visible only in certain lights. In the northern part of the leopard's range in Asia the black phase is unknown, but in the southern, more humid regions, the number increases until the center of their occurrence is reached in Singapore; Assam, Sumatra and the Malay Peninsula being the home of nine out of ten of these animals. I can discover only six references to melanistic individuals of the leopard in South Africa. The name *Felis melas* has been applied to the black leopards, but there is no question of the specific identity of these and the normally colored individuals, since the occurrence of both spotted and black cubs in the same litter has been again and again recorded.

One of the most interesting cases among the mammalia, and one for which at present we can offer no satisfactory explanation, is that of the big-horn or mountain sheep of western North



FIG. 1. Typical examples of (a) the Yellow-rumped Finch, *Munia flavipyrina*, and (d) the Chestnut-breasted Finch, *M. castaneithorax*; and examples (b and c) of *M. flavipyrina* which have partially assumed the plumage of *M. castaneithorax*.
(Courtesy of Mr. Seth-Smith.)

America. Mr. Charles Sheldon writes me as follows concerning the occurrence of the black and the white forms: "I am certain that at some points the same mother has black and white lambs—that a white mother has a black lamb, that a black mother has a white lamb; at such points, however, none of the sheep are pure white or pure black. Moisture has nothing to do with their color. Where the black forms are found, the climate is the same and as dry as in the habitat of the white sheep. On the north side of the Alaskan range the sheep are uniformly pure white, yet living among glaciers and at an altitude where it is much damper than where the black sheep are found. Indeed, the rainfall is almost constant in the mountains in the summer."

While it appears impossible, in the present state of our knowledge, to correlate with more certainty the foregoing examples of melanism and dichromatism, yet we should keep them all in mind while endeavoring to interpret the results of future field studies or experimental researches along these lines. Whether mutation plays a part in the development of any of them or whether all are to be explained as arising by the accumulation of continuous variations, one thing is certain, it is upon one or both of the methods of work which I have mentioned, that we must depend for the elucidation of problems of this character. The collecting of thousands of skins will be of no service nor will the study of those now in our museums be of any direct use. We must have careful and minute tabulation of the ecological conditions under which the phenomena under discussion appear, correlated with the effects of similar, as well as intensified and modified, climatal and other factors, upon individuals under constant observation.

PART III.—SPORADIC MELANISM.

Many records of casual or sporadic melanism are scattered through ornithological literature, of which I shall cite only a few. In 1876 Mr. Ruthven Deane wrote that "melanism is of exceedingly rare occurrence, and but five species have been recorded on my list: *Turdus migratorius*, *Colaptes auratus*, *Melanerpes erythrocephalus*, *Oryx virginianus*, and *Uria grylle*." Later, in 1879, he adds the Carolina rail to this list, and since then other writers have considerably increased the number of birds observed in a melanistic state, such as *Mniotilta varia* and *Strix flammea*. Many of these records have reference to wild birds, others to individuals bred, or at least reared, in captivity.

Melanism in cage-birds has received such desultory attention that as regards food, temperature and other environmental conditions, we are as much at a loss for definite details as in the case of wild birds.

Elliot Coues, W. B. Barrows, Walter Faxon and others have described melanistic American robins in captivity, some of which were congenital in the character of their abnormal coloration, while in other cases the dark plumage was assumed gradually moult by moult. In one bird, the normal plumage appeared during one moult, sandwiched in between melanistic moults, and when examined after death, the bones of this bird were found to contain only one-third of the normal amount of calcium phosphate.

Another robin which became "as dark as a European black-bird," was confined in an aviary built like a greenhouse and sloping south, a condition which might indicate that the bird lived in an atmosphere of considerable humidity.

In an article on "Notes on Melanism and Albinism in Birds," by Dr. A. G. Butler, the theory is advanced that melanochroism in old age is the result of unusual constitutional vigor. He instances a song thrush which had lived in captivity for sixteen years and had become quite black. Elsewhere he says that among thrushes and skylarks which have lived long in captivity melanochroism is not uncommon.

He does not believe that food has anything to do with melanism in captive birds, even doubting whether there is any truth in the oft-quoted case of darkening bullfinches by feeding them upon hemp seed. On the other hand, Distant quotes from Hasting's notes, that not only bullfinches but skylarks and other birds become black when kept upon a diet of hemp.

As a direct cause of local melanism in an individual bird, Dr. Butler tells of a female Martinican dove, *Zenaida aurita*, which had been persecuted by other birds until every feather had been removed from the lower back, and when, after removal to a cage by itself, these feathers were renewed they all proved to be perfectly black in hue. Renshaw was unsuccessful in restoring a nonpareil which had moulted yellow, to its normal coloring, by an increase of animal matter in the food.

Among the weaver birds, *Ploceidae*, some species are reported to become frequently melanistic in captivity and Salvadori observes that among doves, *Chamaepelia talpacoti*, when kept in confinement, often becomes partially or wholly black. Besides these there are many other records, all practically worthless on account of the total lack of clear, definite details of conditions.

I know of no definite experiments which have been carried out in respect to the plasticity of pigment supply in the epidermis of birds of any species; hence the results, interesting and significant as these are, of the few experiments I have undertaken, must be considered only as tentative until they receive further confirmation from future experiments by myself or by others.

Paralleling in many ways the results of my experiments on *Scardafella*, is the relationship between the yellow-rumped and the chestnut-breasted finches *Munia flaviprymna* and *Munia castaneithorax*, two members of the family *Ploceidae* or weaver-birds inhabiting Australia. Mr. D. Seth-Smith discusses this in an interesting article in a recent number of the *Avicultural Magazine*. There is little doubt but that these two birds are closely related, since their songs are exactly alike and the young, until three weeks old, are indistinguishable. The adults, however, are radically unlike in coloring, especially as regards the head and under parts. In *M. flaviprymna* these portions are pale creamy-buff, while in *M. castaneithorax* the sides of the face, ear-coverts and throat are blackish, the sides of the neck and body, fore neck and chest pale cinnamon, followed by a black band across the breast. Below this the plumage is white.

In captivity, specimens of *M. flaviprymna* two or three years of age have been known to assume gradually the markings of the darker species. It was observed of one individual after its fall moult, "the throat had darkened considerably and there were very distinct traces of a dark pectoral band." These birds were at first thought to be hybrids, but as the young of *M. castaneithorax* shows traces of the chestnut breast when only six weeks old and is indistinguishable from its parents at six months, the age of the individuals which assumed the new coloration would alone serve to disprove such a theory.

In summing up his conclusions on this significant change of plumage in captive birds, Mr. Seth-Smith says, "My own theory is, that *M. flaviprymna* is merely a desert form of *M. castaneithorax* which, to fit it for its desert life, has gradually lost the conspicuous markings of the latter. The changed conditions of a life in captivity and a more humid atmosphere, however, cause it, to a certain extent, to reassume the markings which it has lost on account of its desert life. Of course only a very few examples, perhaps not more than one per cent., ever do change color. Whatever the true explanation of the change may be, it seems to me that the two forms are *not* distinct species, but only local races, and in classification are only entitled to be ranked as subspecies."

An Australian trapper of large experience in taking these birds says he has never noticed any variation from the normal plumage in the respective habitats of the two forms, so this latter conclusion would seem at least open to reasonable doubt. However, I have elsewhere in this paper discussed in detail the taxonomic side of a condition such as this. By the courtesy of Mr. Seth-Smith I am able to present drawings of the intergradation of the two birds.

PART IV.—EXPERIMENTAL.

The experiments detailed in the course of the present paper are far from complete. They relate only to three species of birds, but the similarity of result in each case and the possible significance, in relation to certain factors of environment, in the evolution of birds as a whole, would seem to justify publication at this early stage. This part of the contribution may thus be considered as only preliminary to future, more comprehensive researches. The experiments were all carried on at the New York Zoological Park with birds living in the collection of the Society, and for the opportunity of making these studies I am greatly indebted to my chief, Dr. William T. Hornaday.

The early stages of the experiments were made under conditions which rendered it impossible to make other than temperature records, but later, hourly readings with a hygroscope showed that, on the whole, the daily humidity was considerably greater than that of New York City. The mean annual humidity of the city is 73 per cent., while the average humidity to which the birds under experimental observation were subjected was 84 per cent. During the warmer months, from April to September inclusive, the temperature averaged that of the city, 68 degrees, while from October to March inclusive, it varied from 60 to 72 degrees.

Hylocichla mustelina (Gmel.), Wood Thrush.—In the spring of 1902 three young wood thrushes, nine days old and well feathered, were taken from a nest and reared by hand. Both parents were seen and were in every respect normally colored. Soon after the young birds were taken, the parents built a second nest and successfully reared another brood. The moult into the first winter plumage was completed by the tenth of September, and a little before this time, about the first of the month, two of the birds were placed in a very humid atmosphere. One of them died shortly afterward from some unknown cause, no lesions being discernible, but the second bird lived two years, when it met its fate at the beak of a pugnacious robin. In the early fall

of 1903 it moulted well, and although, when compared with skins of typical *H. mustelina*, the breast spots seemed larger and darker, yet there was too little difference to be considered, under ordinary circumstances, as more than individual variation. The death of the bird occurred on August 20, 1904, when its moult was not yet completed. Many of the feathers, however, are full-grown, and the remarkable change in amount of color which has taken place is perfectly apparent. (Fig. 2.)

The upper parts are but little changed, the rufous being slightly dulled by the olive tinge which extends as far as the nape. The most radical difference is to be observed in the feathers of the breast and sides. The general aspect of these parts is of a brownish black, variegated with narrow light edges to the feathers. On the breast the white is more apparent, some of the feathers having circular spots of normal size; but on the sides, flanks and under tail coverts, and even in the center of the belly, the black areas are almost confluent as the feathers lie naturally. The primaries and rectrices show a very pronounced lack of pigment—a tendency toward albinism which is unique among my experiments—albinism having in no other case resulted from a prolonged exposure to excessive humidity.

The third specimen of *H. mustelina*, which was taken from the same nest as the other two, is alive to-day, and in every detail is in perfectly normal plumage, having been caged with a number of other thrushes, outdoors in summer and during cold weather in the passerine hall of the large bird house. The food of both thrushes was the same, a mixture somewhat resembling the "mockingbird food" of dealers—a little scraped raw meat and earthworms; meal worms once a week, fruit, lettuce, chickweed and many kinds of berries.

In a natural state, wood thrushes do not show a great deal of variation, although in some specimens the pectoral spots are more numerous and larger than in others. This is said to be especially true of birds from Guatemala, and in an individual from the State of Tabasco, South Mexico, it was so pronounced that Bonaparte, in 1853, described it as a separate species under the name of *Turdus densus*. This shows that, among wild birds of this species, there is at least a slight tendency toward melanism under the effects of warmth and humidity.

Zonotrichia albicollis (Gmel.), White-throated Sparrow.—On the second day of October, 1901, two white-throated sparrows were trapped in the Zoological Park in traps set for English sparrows. They were both, as was eventually determined, males, and, judging from the dullness of the plumage, were young birds

of the year. One of these birds was immediately confined in the superhumid atmosphere of the experimental cage, while the other was allowed the freedom of a large outdoor aviary in company with song sparrows, tree sparrows, juncos and indigo buntings. The food was uniform in both cases, canary and millet seed with lettuce, and some insect food. No hemp was ever given.

In May, 1902, when closely compared, no difference could be detected between the two birds, and when placed together during examination in a cage, it would have been impossible to identify the individuals in order to return them to their respective quarters, if a primary had not previously been clipped from the wing of one.

In the following year, May, 1903, a radical change had taken place in the bird confined indoors. The general effect was much as in the yellow phase of the undulated grass parakeet, *Melopsittacus undulatus*, only in the case of the white-throated sparrow it was a veil of darkness which appeared to be drawn over the normal markings. In October, 1904, both birds having completed their winter moult, they were chloroformed and made into skins.

The white-throat which had lived the three years of its life outdoors is in all respects normal, and, except in minor details referable to individual variation, the bird is indistinguishable from others in my collection.

The other specimen of *Z. albicollis* is melanistic to an extreme degree. The deviation from the normal coloration of these changes may best be appreciated by an examination of the photograph of the two birds. (Fig. 3.)

In the melanistic bird there is a considerable increase in all black and rufous markings, the latter color taking the place of the normal buff, gray and white. On the wings and body there is reduction or even obliteration of all yellow markings, and on the head and throat a similar recessive tendency of the white. It was recorded while making the birds into skins that the mandibles of the melanistic individual were deeply pigmented while the legs and feet were normal in color, and these characters are still conspicuous.

The gray of the breast remains almost unchanged, but there has appeared in this region a number of broad streaks of dark brown, almost black, which at the posterior edge of the gray area become confluent to form a large pectoral black spot. In the living bird these streaks and pectoral mark were especially noticeable, even more so than they are in the skin.



FIG. 2. (a) Breast Feathers of normally colored Wood Thrush *Hylocichla mustelina*;
(b) Breast Feathers of melanistic Wood Thrush.

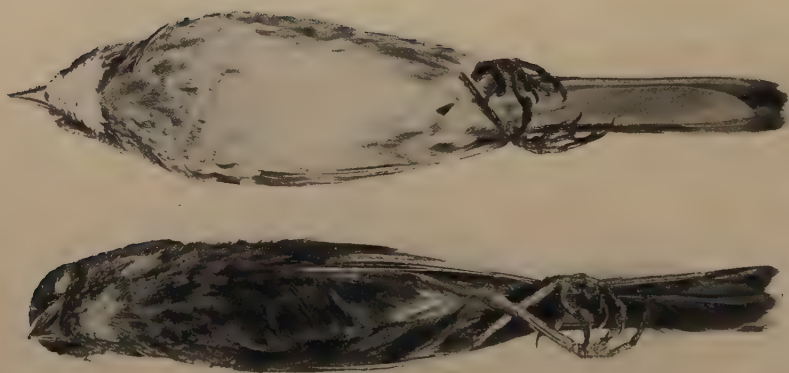


FIG. 3. (Upper) Normal White-throated Sparrow, *Zonotrichia albicollis*; (Lower) Melanistic White-throat, three years in humid atmosphere.

Any speculation as to the significance of these streaks and spot would be of little value, based on this single experiment, but the following facts should be mentioned in this connection, whether or not future experiments give to them greater significance than they now possess. Similar markings, the streaks and pectoral spot, are present in the first winter plumage of *Z. albicollis*, being lost at the time of moult either into the first nuptial or second winter plumage, while they are entirely absent in the adult.

In the closely related *Spizella monticola*, the tree sparrow, a dusky pectoral spot is assumed with the first winter plumage and is a permanent character of the adult birds of both sexes.

Zonotrichia albicollis presents little variation throughout its range which comprises the whole of eastern North America, and no variations of subspecific value have been distinguished by systematists. This lack of variation is probably due to the highly migratory character of this bird, the breeding range being confined chiefly to the region from New York and Michigan northward to Labrador and Hudson Bay. *Zonotrichia querula*, the Harris sparrow of the middle United States, is the species of this genus which shows the largest amount of black in the plumage, the entire crown, throat and part of the breast being of this color. The close relation, almost congeneric, of *Zonotrichia* to *Junco* demonstrates that predominating melanic coloring is at least possible in some members of this section of the *Fringillidae*.

PART V.—EXPERIMENTAL—*Scardafella*.

A—Normal Variation in *Scardafella inca* (Less.)

Inca or *Scaly Dove*.

The genus *Scardafella* embraces a group of small doves which extends as far north as southern Texas and Arizona and south to Brazil. The forms at present recognized by systematists are as follows:

Scardafella inca, Southern Arizona and the Rio Grande valley of Texas, south through lower California and other parts of Mexico to Nicaragua.

Scardafella i. dialeucos, known only from the boundary line between Honduras and Nicaragua.

Scardafella ridgwayi, Island of Margarita and coast of Venezuela.

Scardafella r. brasiliensis,* coast of Brazil, south at least to Bahia. Nothing is known of its distribution in the interior.

* This southern form has not as yet been separated, but for the purposes of this list I have applied this term to the Brazilian birds.

From careful study of the general coloration of over fifty specimens it appears that there is no radical variation in the plumage as a whole in these doves from Arizona to Nicaragua. From this region southward there is a hiatus, if not in actual distribution, at least in the record of any individual of this genus. In Colombia, on the South American mainland, we find *Scardafella ridgwayi*, in which the white of the greater wing coverts is very strongly marked and the dark, scale-like tips of the contour feathers are nearly twice as wide as in the northern birds.

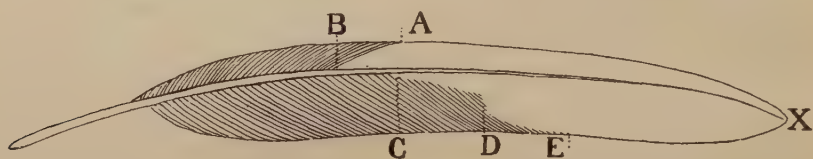


DIAGRAM OF FEATHER SHOWING MEASUREMENTS ON WHICH TABLES ARE BASED.

Disregarding the boundary line of species and subspecies for a reason which will appear later, and carefully tabulating the variations in specimens from different localities, a very apparent grading of certain characters is found from the Arizona to the Venezuelan birds. In Tables I, II, III and IV, which are self-explanatory, I have given the averages for the size of the blackish tips of the outer pair of primaries, and the white tips of the outer (or sixth), fourth and third pairs of rectrices. The figures are all in millimetres and the key to the method of measurement is given in the above figure.

TABLE I.

Geographical variation in the Blackish Tip of Outer Primary of *Scardafella*.

Locality	Number of Specimens	Number of Feathers	A X	B X	C X	D X	E X	Average Area
Arizona.....	10	18	32	41.5	27.3	20	17	27.5
Texas.....	12	22	30.5	36	23.8	19	17	25.2
North Mexico.....	12	23	31.3	36	26.3	19.5	16.5	25.9
West Mexico.....	10	20	31	33.7	19.8	17.5	15.2	23.4
Guatemala.....	2	4	29	32.5	19	17.5	16.5	22.9
Honduras and Nicaragua...	1	2	25	15	14.5	15.5	14.5	16.9
Venezuela.....	9	18	52.3	52.8	25.8	19	17.2	33.4
Brazil.....	1	2	60	60	24.5	20.5	21	37.2

It is to be regretted that so few specimens were available for examination, fifty-seven all told, about ten from each group

locality, except Guatemala (2), Honduras-Nicaragua (1) and Brazil (1). But even with this unequal distribution the results of the various measurements are consistent and serve perfectly to demonstrate what I desire, namely, distributional variation in these wild birds.*

In the case of the dark, distal primary patch, which is shut off from the rest of the feather by the succeeding chestnut, there is a gradual decrease from Arizona to Nicaragua, indicative of the corresponding increase of chestnut. In Venezuelan and Brazilian specimens is found a sudden and extensive decrease of the chestnut; in fact, in the narrow outer side of the vane of the primaries this color is almost, in the Venezuelan doves, or wholly, in the Brazilian birds, lacking.

The white tip of the outer, or sixth, pair of rectrices shows a gradual increase in area southward, from 39.2 mm. in Arizona to 49.2 mm. in Nicaragua. The widest break is between Guatemalan and Honduras birds, being 3.5 mm. In South American birds a considerable reduction occurs—almost to the level of the extreme northern specimens.

The variation in the white of the fourth pair of tail feathers is peculiar. From Arizona to Central Mexico there is a slight but gradual reduction in area—from 16.1 in the north to 13.9 in the latter locality. The Guatemalan, Nicaraguan and Venezuelan birds show a sudden increase—to 25.8, 30.6 and 36.2 mm. respectively, showing that in this pair of rectrices the color variation is far more active and more significant of distribution, and hence climatal effect, than in the outer, or sixth, pair. The size of the white spots in the Brazilian specimen, 24.8 mm., is interesting when we see how closely it approaches the Guatemalan birds, and consider that the two localities, Guatemala and Bahia, Brazil, are about 15 degrees distant from the equator, the one north, the other south, latitude.

The status of variation in the fourth pair is duplicated in the third pair of rectrices, and is even more pronounced, as reference to Table IV will show. The first important fact (as demonstrated by the lessened number of specimens in this Table) is that in two-thirds of the doves from Arizona to Mexico the white tips of the third pair of tail feathers are entirely absent, the proximal brown color extending unbroken to the very extremity of the feathers. Even where the white color is present it is but a terminal fringe, varying in average area from 1 mm. to 2.9 mm. From Guatemala southward, to and including the

*For the use of fifty-six skins of *Scardafella*, I am indebted to the American Museum of Natural History, and for the type specimen of *S. i. dialeucos* to Mr. Outram Bangs.

TABLE II.

Geographical variation in the White Tip of Sixth Pair of Rectrices of
Scardafella—Outer Pair.

Locality	Number of Specimens	Number of Feathers	A X	B X	C X	D X	E X	Average Area
Arizona.....	10	13	52.5	42.3	32.8	33.6	34.8	39.2
Texas.....	12	22	54.2	43.9	39.1	38.2	33.5	41.7
North Mexico.....	12	21	57.1	41.5	35.5	35	31.5	40.1
West Mexico.....	10	17	52	42.6	36.2	32.2	49.3	42.4
Guatemala.....	2	4	60	47.7	42.2	41.5	37.2	45.7
Honduras and Nicaragua...	1	1	62	49	46	45	44	49.2
Venezuela.....	9	13	49.5	43.1	38.6	40.2	42.2	42.7
Brazil.....	1	2	49	42.5	36.5	33.5	33.5	39

TABLE III.

Geographical variation of the White Tip of Fourth Pair of Rectrices of
Scardafella.

Locality	Number of Specimens	Number of Feathers	A X	B X	C X	D X	E X	Average Area
Arizona.....	10	14	20.6	18.6	16.3	16	9.2	16.1
Texas.....	12	21	18	14	15.5	18	12.7	15.6
North Mexico.....	12	22	16.8	14.5	16.5	15.8	8.5	14.4
West Mexico.....	10	13	14.2	13	15.8	16.6	10	13.9
Guatemala.....	2	4	22	25.5	28.7	28.5	24.7	25.8
Honduras and Nicaragua...	1	2	33.5	27.5	32.5	35.5	24	30.6
Venezuela.....	9	13	36.2	35.5	36	37.3	36	36.2
Brazil.....	1	2	25	29.5	24	22.5	23	24.8

TABLE IV.

Geographical variation in the White Tip of Third Pair of Rectrices of
Scardafella.

Locality	Number of Specimens	Number of Feathers	A X	B X	C X	D X	E X	Average Area
Arizona.....	4	8	5.5	3.1	2.1	2.6	1.2	2.9
Texas.....	5	10	3.7	2.9	.7	.8	1.9	1
North Mexico.....	1	2	6	0	0	0	0	1.2
West Mexico.....	5	10	4.7	0	0	2.2	1.4	1.6
Guatemala.....	2	4	10	5.2	7.5	6.7	5.5	6.9
Honduras and Nicaragua...	1	2	8	5.5	4.5	10	1	5.8
Venezuela.....	9	17	8	8.5	8	8.1	9.5	8.4
Brazil.....	1	2	8.5	0	0	5	5	3.7



FIG. 4. Tail Feathers of a melanistic *Scardafella inca*, showing extreme incroachment of the dark pigment, at the tips as well as at the bases of the feathers.

Brazilian specimen, 100 per cent. of the doves show white-tipped third rectrices, and, allowing for individual variation in the Nicaraguan specimen, the ratio of variation is the same as in the fourth pair of feathers; the Venezuelan birds showing the greatest amount, and the Brazilian specimen a reduction approximating the area of the Honduras doves.

As the extreme development of white we find the second pair of rectrices distinctly tipped in several of the Venezuelan specimens, and the dove described from Margarita Island by Dr. Richmond is said to have white on the terminal parts of five pairs, the central tail feathers alone appearing solid brown.

With all this general uniformity of result, the great individual variation should not be lost sight of. In two birds from the same locality, collected within a few days of each other, the variation may be extreme. In one the demarcation of dark brown and white in the rectrices is sharp and clear cut; in the other the colors merge so insensibly into one another that it is difficult to tell where to put the millimeter measure.

Of the entire body plumage, the under tail coverts perhaps show this individual variation to the greatest degree. If there is a distinct terminal mark of black, the feather is apt to be white elsewhere, but the reduction or absence of this mark is often accompanied by an infusion of pale dirty-brown from the base of the rhachis, extending along the shaft line and sometimes discoloring two-thirds or more of the whole vane. This condition, however, is confined to the more northern birds, the colors of the South American doves being remarkably distinct and clear-cut.

In the Arizona and Texas birds there is also considerable variation in the pigmentation of the right and left wing and tail feathers, while in the tropical specimens almost perfect bilateral symmetry is found.

B—The Effect of Humidity on Scardafella inca (Less.).

When typical specimens of *Scardafella inca*—the Inca or Scaly Dove, from Arizona or Mexico are confined in the humid atmosphere for at least six months before the annual fall moult, there is a noticeable change in the new feathers; a slight increase in the amount and intensity of the dark tips, uniformly over the whole body, and a slight blackening of the primaries and rectrices. One individual, even at this first moult, shows a condition adumbrative of the whitened wing coverts which are so conspicuous a feature of the next moult. This bird closely resembles the *Scardafella inca dialeucos* type. At the second fall

moult this general darkening is much more noticeable, and correlated with it there is considerable reduction of the rufous on the primaries and on the lining of the wings. The greater wing coverts are very light, the outer vanes appearing almost pure white in contrast with the adjacent areas of black and dark brown.

Although the considerable individual variation, as shown in greater or less reaction to the humid atmosphere, is very noticeable even in the few specimens upon which I have been able to experiment, yet the general average appearance of this moult under these conditions is not distinguishable from that of a wild bird in the typical plumage of *Scardafella ridgwayi*.

The rose or lilac ground color of the upper anterior part of the plumage remains unchanged, until, in succeeding moults, it is totally obscured by the encroaching melanin pigment; the white of the lower breast remains clear white to the last; the suffusion of pink over the breast loses none of its intensity until completely concealed by the black. In the final stage, attained in the fourth or fifth moults, the chestnut on all the primaries has completely disappeared; the breast feathers, secondaries and even the greater coverts have lost all trace of white, although, as we noticed above, the coverts had become noticeably whiter at the second moult. The last white to remain is a spattering upon the longest under tail coverts and upon the three outer rectrices.

TABLE V.

Primary Change of Coloration Area of *Scardafella* under Humidity.

	<i>At End of Third Annual Month, Jan. 28</i>	<i>First Induced Monthly Renewal Feb. 25</i>	<i>Second Induced Monthly Renewal Mar. 27</i>	<i>Average Increase of Area</i>
Outer Right Primary.....	38		41.6	3.6
Second Right Primary....	37.4	37.8	39.2	1.8
Third Right Primary.....	36	38	39.2	3.2
Sixth or Outer Rectrices..	32.8		33.3	.5
Fifth Rectrices.....	24		29.4	5.4

Table V gives the average areas of the black on the primary tips and of the white on the three outer pairs of rectrices of a bird from Mexico which, under experimentation, had completed the normal third annual moult. It will be seen that the area of the black outer primary patch is slightly larger than in the wild Brazilian bird (Table I). The white on the outer rectrice of

the captive dove shows an extreme individual variation in the direction of reduction, no greater, however, than exists among wild individuals. The chief interest of Table V lies in the comparison of the measurements of the feathers which came in after those first recorded were pulled out. Three such successively induced renewals of feathers show a regular change in extension of color area—in the case of this bird of the third regular moult, an *increase*, both of the primary black patch and of the rectrice white. Taking the outer primary we may judge of the ratio of increase between the regular annual moults, and the induced monthly feather renewals, by the following comparison:

	<i>Wild Bird from North Mexico</i>	<i>At 3rd Annual Moult of Captive Dove</i>	<i>Feather Renewal One Month Later</i>
Area of Outer Primary Patch	25.9	38	41.6
Average Increase		4	3.6

This indicates that the increase of pigment in one month in an artificially induced renewal of the feathers is about the same as that occurring in a feather which comes in as a result of the normal annual moult. If this comparative scale of increase of melanin should hold good, plumage as black as in the sixth year individual about to be mentioned could be obtained in almost the same number of months by monthly feather renewals. No test of this has yet been made.

Table VI relates to a dove which has completed six regular annual moults in the humid atmosphere, and has become almost entirely black. At the examination of January 28th, a very faint trace of rufous was observable near the center of the third from outer primary, but in the new feathers observed March 27th, all

TABLE VI.

Secondary Change of Coloration Area of *Scardafella* under Humidity.

	<i>At End of Sixth Annual Moult, Jan. 28</i>	<i>Succeeding Induced Feather Renewal, Mar. 27</i>	<i>Average Decrease of Area</i>
Outer Right Rectrice.....	29.4	28.4	1
Fifth Right Rectrice.....	25	23.8	1.2
Fourth Right Rectrice...	11.2	4.6	6.6

trace of this color had disappeared. Hence data for comparison is confined to the rectrices. Besides the three outer pairs of these feathers, no white was left on the dove except an irregular whitish-gray blotch on the longest left under tail covert.

The most interesting fact brought out by the monthly feather renewal of this black dove is the *reduction* of the white on the rectrices, instead of an *increase*, as was the case with the dove in the third moult.*

The most logical explanation would appear to be that excessive humidity causes, not only an increase but, especially during the first few moults, a concentration of the melanin—resulting in a segregation of the black and white and consequently an increase in area of the latter. This condition is at least paralleled in wild Arizona and Venezuelan specimens (*vide* Table I). If, however, the humidity continues to act, and here we get beyond the stage of any wild *Scardafella*, a point is reached where further concentration of melanin is impossible, and the overproduction of granules is forced into the surrounding epidermal structures. (Fig. 4.)

From now on a gradual *reduction*, (Table VI), of the white area takes place until the dark hue is everywhere predominant.

It may here be stated that in a number of cases measurements were made when the feathers had just broken from their sheaths, and again, eleven months later, just before the annual moult, and no change was apparent. *This eliminates from these experiments any theory of increase of melanin without moult.*

I have elsewhere recorded the fact† that the pigmentation of the choroid coat of the eye is, at least in owls, correlated with the pigmentation of the plumage, the choroid of a dusky horned owl being very strongly pigmented as contrasted with the all but absence of pigment in a snowy owl. The optical fundus of a small dove such as *Scardafella* is very difficult to observe, and thus far I have been able to make out only the grosser details. But in my completely melanized specimen the great increase of pigment over a normally colored *Scardafella inca* is very noticeable, and is interesting as showing that the pigmentation of this part of the eye is as plastic as that of the plumage. It is, however, only what we should expect when we recall their identity of origin; the feathers being epidermal structures arising from an induration of epidermal papillae containing a vascular core, while

* Fig. 4 shows that this restriction of the white of the rectrices is not only from the proximal part of the feathers, but at the tips where there has appeared an area of encroaching black.

† "Owls of the Neartic Region," Eleventh Ann. Rep. N. Y. Zool. Soc.

the epithelial pigment of the choroid is as truly epidermal, tracing its derivation, in the embryo, from the involuted epiblast of the medullary canal.

With the sixth moult, experiments have for the present ended, but the blackest dove now in the collection exhibits an interesting condition which may, in future work, prove as significant as it was unexpected. In wild specimens of *Scardafella inca* there appears to be no trace whatever of any iridescence or metallic tints, the darker tips of the feathers being a dull and lifeless brown. In the Venezuelan *S. ridgwayi* the largest dark-tipped feathers show, in a very favorable light, a trace of dull greenish or bluish sheen.

In the darkest bird under experiment, this metallic color is strongly developed, and in a most interesting way. The feathers of the lower parts show little iridescence, and this of a bronzy character, but above, the plumage is as iridescent as that of any East Indian fruit pigeon. The entire back and rump are similar in hue, each feather having a broad tip of iridescent bronze, while the remaining exposed part of the feather is of a brilliant green, this tint extending down along the rhachis as a shaft stripe, a little way into the distal bronze portion. The primaries and outer secondaries are dull black, but on the inner secondaries, coverts and scapulars the most brilliant iridescence is found. On some of the feathers blue and green seem arranged in cross bars, but, on the whole, the metallic coloring is irregular, the entire feather changing in color as the angle of incidence of the light is changed. This alar distribution of iridescence becomes significant when we consider the occurrence of metallic color in the plumage of many genera of doves—some rather closely related to *Scardafella* and others separated by considerable structural differences.

The rather closely related genera *Columbula* and *Chamaepelia*—ground doves of the Neotropical Region—are ornamented with metallic colors on the wing coverts; in the first mentioned forming a band of steel blue on the lesser coverts, and in *Chamaepelia* being arranged as a number of spots and blotches, both on wing coverts and inner secondaries. These spots are of various colors, as bronze in one species and purplish-green in another. In a future paper I shall discuss variation in the genus *Chamaepelia* and the effect of artificially changed conditions of environment on these metallic patches; but here I mention them only to show the tendency, in certain groups of doves, to iridescence on the wing coverts. In our northern mourning dove, *Zenaidura macroura*, the wing coverts exhibit dark spots which are glossy

but hardly metallic. As the opposite extreme, in an otherwise rather dull-hued bird, I may mention *Ocyphaps lophotes*, the Australian crested pigeon, in which the greater wing coverts are a shining, bronzy green, while the inner secondaries glow with the richest iridescence—changing from purple to blue.

Until my observations have been supplemented by microscopic work I shall hazard no speculations as to whether, in *Scardafella*, the continued effect of humidity brings about an actual change of structure in the barbs of the feathers, when the dull-brown or white color of the wing coverts gives place later, in the same individual, to metallic tints. If so, according to Gadow's theory, this would be iridescence by refraction. On the other hand, iridescence may result merely from the abnormal abundance and extreme concentration of spherical melanin granules producing the effect of Newton's rings, or thin-plate interference colors. The latter would seem the more probable theory, apparently supported by the careful work of Strong on the domestic pigeon. I have not yet had the opportunity of verifying this in the case of *Scardafella*.

C—Summary of the Effects of Humidity.

1. When typical specimens of *Scardafella inca* are confined in a superhumid atmosphere, a radical change in the pigmentation of the plumage takes place with each succeeding annual moult.

2. A change, apparently similar in extent and direction, results from an artificially induced monthly renewal of the feathers.

3. The change at the first annual moult brings the bird close to the *Scardafella inca dialeucos* type.

4. At the second annual moult, the plumage approximates either the Brazilian type or the typical *S. ridgwayi*, the succeeding changes being unrepresented by wild species of the genus.

5. Intrinsically the change is at first a segregation and intensification of the melanin, resulting in a clearing up and extension of the white or whitish areas.

6. A period of equilibrium later ensues, until the increase of melanin is such that it begins to encroach upon the white areas, this continuing until all trace of white has disappeared.

7. Coincident with this intense blackening of the plumage part of the epidermis, occurs an increase of pigment of the choroid coat of the eye.



FIG. 6. Side view of *Scardafella* doves shown on page 31.

8. When the concentration of the melanin has reached a certain stage, a change in color occurs, from dull dark brown or black to a brilliant iridescent bronze or green.

9. This iridescence reaches its highest development on the wing coverts and inner secondaries, where, in many genera of tropical and sub-tropical doves, iridescence most often occurs.

10. All these changes take place by continuous variations, and there is no change of color without moult.

D—Significance in Respect to Direction of Evolution.

The increase of pigment in a single individual under humidity during a comparatively short period of time, and the subsequent correlated development of metallic tints, assume a new importance when we consider that, in these experiments at least, mutation and natural selection have no place.

In a recent paper embodying some interesting comparisons of many wild species of doves and pigeons, Prof. C. O. Whitman advances the theory that the various gradations of color patterns, such as those on the wing coverts, are hints of closer or more remote biological relationship, and the apparent directive progress of the character he explains by orthogenetic variation, affected to a certain extent by natural selection, but not by mutation. He says: "If a *designer* sets limits to variation in order to reach a definite end, the direction of events is teleological; but if organization and the laws of development exclude some lines of variation and favor others, there is certainly nothing supernatural in this and nothing which is incompatible with natural selection. Natural selection may enter at any stage of orthogenetic variation, preserve and modify in various directions the result over which it may have had no previous control."

Setting aside discussion of the orthogenetic theory itself, we find that Prof. Whitman is able to offer in regard to the actual transition of one stage of coloring to another, evidence only from comparison of wild species, or from young and adults of some one species. He says: "But is there any direct proof that the transformation is actually making progress to-day? May not these transitional steps go on appearing generation after generation, without ever making any permanent progress? We have to concede that we can not follow the processes that reveal themselves in steps. We can at most only see what is done—not the doing. We are entirely in the dark as to the time required to carry the change through a single row of feathers."

Perhaps the most interesting part of Prof. Whitman's paper is that relating to eight years' experimental breeding of domestic pigeons. In the offspring of checkered birds, by careful selection, birds with fewer checkers were produced, these checkers gradually merging into three and two bars, and at last into one, following which came total obliteration of dark color on the wings. It was found impossible to reverse the process, that is, to obtain doves of the checkered type from typically barred birds. Hence the author assumes that "the direction of evolution can never be reversed."

In comparing these statements with the results which I have obtained with doves under the influence of humidity, there is one fact of which we must never lose sight—perhaps the most important factor with which we shall have to deal, when future experiment enables us to stand on firmer ground. This is, whether we are dealing with *acquired* or with *congenital* characters. In the case of the individual *Scardafella* doves there is certainty that the seeming atavistic characters are *acquired*.

Nine genera of *Columbiformes* are found in the United States, one of which, *Ectopistes*—the passenger pigeon—is autochthonous, at least in its present distribution, while *Zenaidura*—the mourning dove—extends southward only as far as Panama. The remaining seven are highly developed in the Neotropical Region, hence we may be reasonably certain that the Columbine element in the North American fauna is of tropical origin.

This would indicate that those forms of doves and pigeons which barely extend over our southern border have been derived, more or less recently, from tropical types. Accepting this as a fact, then in reproducing a tropical atmospheric environment for our *Scardafella inca* and by this means rehabilitating it in its ancestral plumage, we apparently demonstrate an exception to the assertion of Prof. Whitman that "the direction of evolution can never be reversed."

On the other hand, the *modus operandi* of this atavistic change seems to support that author's orthogenetic theory, in so far as the recapitulation follows along the same lines (1) as in related genera of doves, and (2) in the identity of the details of the change in several individuals. This indicates that this humidity-induced variation is neither fortuitous nor directionless.

Interesting and significant as the results are, they but open up innumerable new vistas of unexplored fields. If the melanic doves were bred, would there be any trace of inheritance of these

acquired color characters? If subjected to an environment of extreme dryness would *Scardafella ridgwayi* assume the plumage of *S. inca*? Would other melanizing factors than humidity, such as hemp food, bring about similarly orthogenetic series of changes? * Is *Scardafella* especially plastic in response to experimentation, or does this plasticity reflect very recent variation in the feral state? What would be the effect of applying these conditions before the adult plumage is acquired?

Have we in these unexpectedly radical changes of plumage under humidity any hint or clue to the annual changes of many migratory birds, such as the male scarlet tanager, indigo bunting and bobolink, which assume brighter colors after a winter in the humid tropics? If so, why are the females immune from such influence? Considering Prof. Whitman's law, under these conditions of experimentation, can the direction of evolution ever be *anticipated*? These and a hundred other important aspects of the problem all await solution.

In regard to the all-important question of the inheritance of somatic changes produced by external factors, we have for comparison the affirmative facts given by Fischer, who produced moths of dark colors by exposure to a low temperature and reports that the offspring of two of these moths were also dark; and the negative results of Tower, who after experiment upon ten lineal generations of *Leptinotarsa* declares that "it is clearly demonstrated that the somatic variations in color are not inherited, but that they are fluctuating, transient, and due solely to environmental stimuli which accelerate or retard color development." Tower explains the affirmative result by the apparently logical reasoning that during the period of experimentation in the case of the lepidopterous insects, the germ cells were in the more sensitive stages and hence were directly affected by the stimulus of cold, this being not the case in his own experiments. If this is true, we have yet to await the demonstration of the inheritance of a true acquired character—a phenomenon which will doubtless never be forthcoming.

E—Correlation with Natural Selection.

The question will at once be raised by some, that my experiments, as far as they go, indicate that natural selection has little or nothing to do with such phenomena as protective coloration.

* As far as my experience goes, a diet of hemp produces in *Scardafella* an irregular blotchy melanism, very different from that induced by humidity, but this is based on only one individual.

tion and mimicry. But I think this is not the case. Even among the four or five individual doves, upon which the experiments were carried out, there is a noticeable variation in the readiness of response to the unusual conditions; in the course of the first two moults one individual becoming melanized to a greater extent than the other doves.

If Arctic animals are white *solely* because of physiological reaction of the pigment-producing tissues to cold or other environmental factors, why should the musk ox (*Ovibos*) and raven (*Corvus*) be such conspicuous exceptions to all the other terrestrial vertebrates of those northernmost regions? We may correlate with this, the fact that, owing to their food and powers of defence, these two creatures have least need of either protective or aggressive coloration.

If natural selection can not and does not sometimes entirely annul this physiological reaction to temperature and humidity, why does the snowy owl not change in summer like the ptarmigan? and why does the mink retain its dark pelage throughout the year, while its near relative, the northern weasel, becomes almost wholly white? It is said that Arctic animals when brought into warmer regions sometimes become darker in hue, but, as far as I know, the reverse has not been observed.

The sporadic appearance or artificial inducing of melanism in a single individual under humidity may be explained, and probably correctly, as merely the result of intensified action of the pigment-producing enzyme or unorganized ferment. But this becomes of profound interest and importance to the evolutionist when we consider it as one, among other widespread factors in the production of new races and species. The fact that such radical changes in appearance can be brought about—not only by the well-known method of careful selection through many generations, and with definite exclusion of the very improbable theory of the change of color in the plumage without moult—but by comparatively rapid, cumulative, apparently orthogenetic, acquired variations, will cause many of us to consider a revision of our ideas as to the length of time necessary for the formation of new races and species, when these are based on color characters alone. And this without the aid of De Vries' theory of mutation by one profound saltation, whatever the part this may have played under other, as yet imperfectly understood, conditions.

The absence heretofore of all evidence of such rapid, continuous variation as shown by these experiments, has naturally led to statements such as the following: "The gradual evolution



FIG. 5. Ventral View of (a) Typical wild *Scardafella inca*; (b) Type specimen of *S. i. dialucos*; (c) Typical wild *Scardafella* from Brazil; (d) Typical wild *S. ridgwayi* from Venezuela; (e) *S. inca* after three moults in a superhumid atmosphere.

of a permanent change of color, such as marks geographical races or representative species for example, must obviously be due to the long-continued action of the environing conditions upon the whole organism."

F—Correlation with Taxonomy.

Up to the present time, considerations of ontogenetic, as compared with phylogenetic characters or "species" have been of little import to the taxonomist, considered strictly as the delineator of living species. His business is to perfect, as nearly as possible, the forging of the nomenclatural handle by means of which we may grasp present conditions of life on the earth, and which enables us intelligently to communicate to one another the results of our studies.

To speak in hyperbole—it has not directly concerned him whether the color of *Scardafella* is as fleeting as the life cycle of a single feather, or as permanent as the power of flight in these doves. Through the processes of evolution both color and flight were acquired in past time—whether at the preceding moult or during the Jurassic Age; whether by a rapid chemico-physical process or by gradual synthetic variation through geological ages—has made no difference in the delineation of species living on the earth to-day. Nevertheless, in the words of Dr. Merriam, "a knowledge of the *degree of difference* between related forms is infinitely more important than a knowledge of whether or not the intermediate links connecting such forms happen to be living or extinct."

Regarding the characters of ontogenetic species Dr. Jordan writes: "Perhaps our ornithologists will some day test their species and subspecies by a test of the permanence of this class of characters. No doubt we should drop from the systematic lists all forms which may prove to be merely ontogenetic, all whose traits are not fixed in heredity." In answer to this Dr. Allen says, "any attempt to distinguish ontogenetic species from other species or subspecies tends to confusion of ideas rather than to any useful discriminations."

Of course, at best, only a small proportion of living forms could be so successfully subjected to transplanting or to experimental conditions, that their exact status in an onto-phylogenetic classification could be ascertained. Nomenclature is avowedly artificial and imperfect: its permanence, dependent on the existence of the historical period of the human race; its advance, on the increase of knowledge. When the new science of experi-

mental biology has developed to a point where it can clearly account for, if not indeed anticipate, results of experiment upon wild creatures, there seems no more objection to admitting such evidence than that obtained through embryology, anatomy or palaeontology. The development of birds from a reptile-like type is not the less certain because we know of only two specimens of *Archaeopteryx*; and, although comparatively few types of living organisms can be experimentally tested, the resultant evidence, when we can clearly interpret it, is of none the less value.

The crucial point seems to be that, while we should use this evidence to the utmost in unraveling the intricate processes of evolution, and in understanding the past history of the wild living forms, or as we call them species and subspecies, as now defined—yet to alter our entire list of species, discarding all forms—which are ontogenetically interchangeable under experimentation or in a new environment, by analysis or synthesis as the case may be, is no more reasonable than to discard a genus of living creatures because palaeontology reveals more delicate gradations between it and a second living group—isolated by the present conditions of life.

If I take an individual *inca* which, under certain conditions, has changed to a darker form, more extreme than *ridgwayi*, and apply to it the term *nigra*, I may claim that it represents a good ontogenetic species, isolated by moult from any other species. As long as the conditions remain the same, my new species remains unchanged, perhaps for years, but if it moults into a still blacker form, the status of *nigra* would revert, theoretically, to the condition of an extinct fossil link; but practically, this distinction would be inimical to the usefulness of classification. It would mean recognizing one of the past moults of *the individual* as a prototype or ancestral connecting link!

The boast of our scientific nomenclature is that it is as near the natural order of evolution as possible and yet remain a help to working naturalists. When this most important function is imperilled by the naming of innumerable variations within a narrow field, the more conservative biologists rightly protest. The same would result if, in the case of *Scardafella*, having transmuted an individual *inca* into *ridgwayi*, and thus proving the differentiation to rest merely upon ontogenetic characters, the name *ridgwayi* should be stricken from our lists, regardless of the fact that there is apparently a geographical hiatus between the two forms in a wild state. Differences between the two species in habits, nidification, courtship or notes, could not be expressed were both swamped under one name.

Theoretically, and to the evolutionist in the widest sense of the word, (for whose use nomenclature, to all intents and purposes, solely exists), the results of experimental biology are of greatest importance, but the forms thus artificially produced should no more be added to the lists of natural species than should the brahmas and plymouth rock fowls of our barnyards. As in so many scientific questions there is a border-land difficult to define, and in this case it consists of the forms transplanted by man in more or less distant times, which have developed new characteristics (as in the Porto Santo rabbits). In my opinion, none of these should be placed on our lists without being stigmatized as to the human influence involved.

To those of us who are primarily students of the broader aspects of evolution, the results of experimental biology appear most valuable in giving clearer insight into the conception of the ideal and only *natural* classification—one arranged in the three planes of space.

G—Correlation with Organic Selection.

Any correlation of the results outlined in the present paper with the various theories of evolution must be tentative in the present state of our knowledge. Keeping this in mind, the following explanation appears among the most logical and probable.

The results of the effects of humidity are open to the following interpretations: (1), they may reflect a reversal of evolutionary variation along the line of least resistance, from *inca* through *dialeucos* to *ridgwayi* and beyond; (2), they may indicate an advance in evolution, paralleling the condition found in wild tropical types; (3), they may represent merely indefinite fortuitous variation, brought about by a change in the environment. Whichever we choose for the present as the most reasonable working hypothesis, it seems to me that we have an excellent argument in support of the theory of organic selection.

We know that melanin is a non-ferruginous non-hematogenous intrinsic pigment, absorbing the violet rays which, at least in ourselves, are particularly irritating to the skin. If the same phenomenon holds true of birds, an increase of melanin in the epidermal structures would certainly prove of advantage in a hot moist climate, and might thus be considered an adaptive structural response.

In the case of *Scardafella* we see an instance of remarkably rapid physiological reaction to a radical change of the environment. In a state of nature such a change might be imagined as

taking place under conditions approximating those of the formation of the Salton Sea, in the Colorado desert in southern California, where the sudden appearance of a large body of water in an arid region might be accompanied by a considerable increase in the relative humidity. If any change in color in the plumage of the local species of dove should prove of adaptive value, in influencing even to a slight degree the vitality of the birds, the species would at once benefit. Natural selection would exert an important influence in the elimination of those with less plastic pigment-forming enzymes, or it might operate in an antithetical way by raptorial elimination of the darkest, most conspicuous, individuals. Be this as it may, we can be reasonably certain that this ontogenetic modification is only somatic, and that the offspring would acquire the dark color anew only with the first few moults. Until some of the problems offered by *Scardafella*, mentioned on page 33, have been solved, we have no means of telling how soon or in what manner this modification would become congenital; or, in other words, would be transferred from an acquired to an inherited character.

But this is not necessary to the present argument, that, in the *Scardafella* color modification, organic selection finds strong support. If the new character, ontogenetically acquired, is in any way adaptive, it might easily be the means of preserving the species until phylogenetic variation had impressed it upon the race.

That we have much to learn concerning these greatly disputed classes of variation is shown by another phase of this very experiment. We have seen that the specific and apparently permanent color distinction between *S. inca* and *S. ridgwayi* is, in reality, so plastic that a year or two of superhumidity will annul it. Thus two species widely separated by a geographical hiatus may actually be differentiated by the most evanescent of acquired characters. So, while theoretically explainable by organic selection, yet we see that a character, which few evolutionists would have considered apart from regular inherited, specific characters, might, after we know not how many years and generations, still prove to be of the most superficial and transient nature.

Bearing in mind the Porto Santo rabbits and the probably considerable time during which *Scardafella* has inhabited Mexico, we can easily see that an ephemeral, acquired, yet adaptive character, might render life possible in a region otherwise untenable, through a sufficiently long period of time for congenital variation plus natural selection to bring about skeletal and other modifications of generic, if not indeed of family, importance.

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